# The Role of Attention in Learning About Odorants

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*The goal throughout this period was to understand the neural mechanisms mediating chemosensory responses and related behavior. At the same time, it was the behavior that was providing insight to the mechanisms. The behavioral approach was an* exciting game of wits [emphasis added]. *It proved to be a powerful tactic, and many of its findings were subsequently shown by electrophysiology to be gratifyingly accurate.*

—*Dethier (1990)*

## Introduction

Animals must solve several kinds of problems in relation to identification and location of food or mates. One fundamental problem involves recognition of the types of stimuli that help to predict the spatial and temporal occurrence of such resources (Smith, 1993). These stimuli occur in complex, changing backgrounds that might disrupt recognition of critical stimulus elements. Thus the task at hand for the sensory system is to filter out the less relevant background information in order to extract those elements that reliably provide information about the identity and location of the resource (Hopfield, 1991).

To perform this feature-extraction task, nervous systems must be capable of devoting as much of the system's processing capacity as possible to the essential elements of the signal. One approach is illustrated by the pheromone systems of moths and cockroaches (Masson and Mustaparta, 1990). In those animals, specific neural pathways are devoted to processing information about a very restricted set of odorants (Hansson *et al.,* 1991;

Rospars and Hildebrand, 1992). Particular pathways, beginning with the peripheral sensory cells, are typically narrowly tuned to one element of a pheromone mixture or to the appropriate mixture itself. The information content of pheromones is stable over evolutionary time, hence more of the olfactory system's processing capacity can be dedicated (hardwired) to detection of the restricted range of elements in the pheromone.

Feature extraction is a more complex problem for odorants that are not pheromone-like in their information quality; that is, their meaning can change rapidly within the lifetime of any given individual (Smith and Getz, 1994). For example, foraging honey bees learn to associate floral odorants with the nectar and pollen resources that are necessary for colony survival (Menzel, 1990). Thus, as has now been shown in many studies, a floral odorant can act as a conditioned stimulus (CS) to train honey bees by Pavlovian and instrumental/operant conditioning procedures (Bitterman *et al.,* 1983). Odorant information, which together with general distance and direction information is transmitted among individuals during dance recruitment, enables recruits to identify which among several types of flowers in a locale are providing the resource at any given time (Frisch, 1967). The problem is that floral odorants are mostly complex mixtures of dozens to hundreds of component odorants, and the exact nature of the blend can change from flower to flower or within a flower across short periods of time (Pham-Delegue *et al.,* 1989; Knudsen *et al.,* 1993).

In fact this problem of blend recognition is a general one faced by all animals that have even a rudimentary sense of smell. Many biologically relevant odors are mixtures of at least several components, and a number of physiological and molecular-level processes might limit an animal's ability to perceive component odorants or submixtures in a blend (Dionne and Dubin, 1994). Odorants in a blend interact, at least in vertebrates, with potentially thousands of receptor types embedded in sen-

sory cell dendrites (Buck and Axel, 1991), and cells that express a particular type of receptor project to the same glomeruli (Vassar *et al.,* 1994). Recent investigations of sensory physiology have shown that odor molecules interact with these receptors to produce several nonadditive effects when odorants occur in a mixture (Ache, 1989, 1991; Atema *et al.,* 1989; Getz and Akers, 1995; Michel and Ache, 1994). Such effects include mixture suppression, which is the decrement of response in one type of cell to a specific odorant due to the presence of additional odorants in a blend. Furthermore, synergistic interactions may recruit new cell populations to respond to the blend even though they show little or no response to the component odorants. Therefore, it is likely that a blend of two or more odorants may take on perceptual properties that are unlike those of any component, and any recognizable quality of the components might be diminished.

The picture presented thus far presents a tremendous challenge to our understanding of learned odor recognition. Olfactory signals are characterized by the production of an input signal that must have an extraordinarily high number of dimensions, and addition or deletion of components in a blend can qualitatively change how the blend is perceived. If, therefore, the perceptual qualities of a blend are so dramatically affected by perturbations in the presence or ratios of components, then how does a bee, or for that matter any animal, recognize the "same" odor despite the high degree of variability across space and time? It may be that different flowers, or even the same flower at different times of day, have slightly different compositions of odorants than those that were experienced at an earlier time. What is needed is a sensory processing system that exhibits "graceful" degradation as the stimulus is altered.

Therefore, an important conceptual problem that faces us in our understanding of the olfactory system is this: How do animals generalize from one experience with a learned odorant to the next experience even though the two presentations may differ? The problem of generalization has played a central role in learning research (Kalish, 1969; Shepard, 1987). Indeed no two presentations of any CS are alike even under controlled laboratory conditions (Kalish, 1969). If an animal were to focus on identification of only the exact CS used for training, it might risk making an inappropriate response on a later presentation. That is, in the extreme case a bee might revisit only the same flower it just depleted of nectar (Smith, 1993). It is easy to understand how that could be fatal to an animal in the short or the long term, especially when such learning helps to predict an imminent encounter with a predator (Hollis, 1984).

One means of dedicating computational resources to particular elements of a complex signal—that is, ensur-

ing that animals generalize to the most relevant aspects of a signal—can be loosely categorized under the general phenomenon of "attention" (Logan, 1992; Holland and Gallagher, 1995). This term subsumes many kinds of processing systems that have at least one fundamental feature in common—the processing capacity can be flexibly dedicated and rededicated to different elements as the information value of those elements rapidly changes. The concept of attention can involve differing degrees of complexity and flexibility in species with different capacities inherent in their central nervous systems. But in all cases it helps animals to filter and process the more relevant elements of a signal that is composed of a complex and changing mixture of elements. The ability to attend to specific elements of a signal while learning other elements performs essentially the same function as the pheromone system described above: it allows animals to attend to the informationally more relevant signal elements while filtering out less relevant ones. This kind of attention system is most relevant for signals that have rapidly changing information content, such that processing capacity cannot be dedicated developmentally as it is in the pheromone systems.

In the spirit of the above quote, it is the point of this contribution that behavioral studies indicate that mechanisms exist by which animals can "extract" component information from odors made from mixtures of two or more components. One such behavioral paradigm, termed "blocking," is highlighted. Paradigms such as blocking have been employed to study how animals learn about mixtures of stimuli from different sensory modalities. But paradigms can also be effectively used to study processing within modalities. Using information from these behavioral studies, we can now make testable predictions about the nature of signal processing, beginning with sensory receptors and proceeding inward, that can explain how animals solve the variance problem with odors. Many of these studies highlight what amounts to an ability to flexibly devote neural computational resources to processing one or a few signal components. That is, they describe processes of attention, which may vary in complexity across taxa. But first, it will be useful to review a more commonly accepted model of olfactory processing and generalization.

### The Problem of Stimulus Generalization

As defined above, the essential problem is to determine how animals generalize from one odor to another so as to appropriately respond to an odor that is slightly different from the one to which they were trained. Stimulus generalization can arise and vary among individuals as a result of a variety of factors (Kalish, 1969). A typical means for studying generalization would be to train sub-

jects to a single CS, for example, a tone, and then test the same subjects by varying some dimension of the CS, such as frequency or intensity. In such a protocol generalization, which is defined as a response to a stimulus that represents an alteration in some property of the CS, is frequently presumed to occur because the dimension along which the CS is varied (*e.g.*, frequency, wavelength, intensity) is represented in the peripheral and central nervous systems. The dimensions represented in the nervous system can be set up developmentally—that is, by the array of receptors expressed across sensory cells (Buck and Axel, 1991)—as well as by associative or cognitive mechanisms that form new dimensions as a result of experience (Shepard, 1987).

Generalization in the olfactory system has been studied in honey bee workers trained to respond to a pure odorant CS (Smith and Menzel, 1989; Smith, 1991). The same subjects are subsequently tested with odorants possessing the same oxygen moiety (*e.g.*, ketone, aldehyde, or alcohol) but different carbon chain lengths, or with odorants having the same chain length but different oxygen moieties. For most odorant types fairly smooth generalization gradients can be established. That is, subjects respond very strongly to the CS and slightly less so to an odorant similar in structure to the CS but varying along some dimension. The response becomes progressively weaker as the structure of the molecule is changed even more along one or two dimensions. Similar data, albeit using electrophysiological responses of mitral cells, have been obtained recently in the rabbit (Mori, 1995).

Generalization from a mixture to one of its submixtures or to one of the components can occur *via* the same type of mechanism as for pure odorants if relevant dimensions can be defined in the nervous system. For example, peripheral sensory interactions between odorants in a binary mixture ($A + X$) could give rise to a neural representation for the mixture that is different from those for either component ($A$ or $X$ alone). That is, the neural elements activated by $A + X$ could be qualitatively different from what would be expected given a simple summation of the elements activated by $A$ and $X$ alone (Pearce, 1994). Indeed such "configural" elements from a mixture could be the ones to which relevant associations with an unconditioned stimulus are made. The greater the difference between the sensory/neural representation for the mixture and those of the two components, the weaker the generalization from the mixture to either component (Fig. 1A).

This type of model was proposed by Hull (1952; see review in Pearce, 1987) to explain "overshadowing" in the same terms that were used to account for generalization within a defined dimension to a single CS. A typical overshadowing experiment would compare principally two groups (Table IA). One group (OVERSHADOW) is
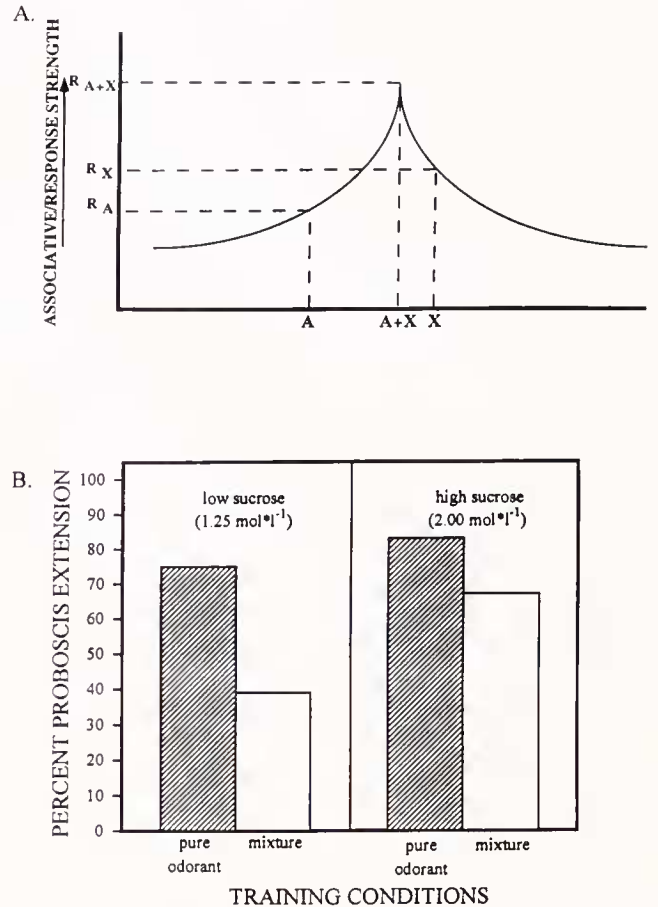


Figure 1. Overshadowing due to afferent interaction at the sensory receptors/cells. (A) Schematic diagram of a model in which afferent interaction between $A$ and $X$ occurs to give rise to a sensory input that is unique to the $A + X$ mixture. The mixture-unique pattern defines a point in a sensory input pattern at which a strong associative strength exists with the neural representation of a reinforcer. The response strength to either $A$ or $X$ would be a function of the similarity of the neural representations of those elements to that of the mixture. The "sensory" space is shown here as a single dimension for simplicity; but it is most likely to be multidimensional in character (Shepard, 1987). (B) Overshadowing of odorant $X$ conditioned in a mixture relative to when conditioned as a pure odorant. Four groups of honey bee workers were conditioned *via* standard protocols for proboscis-extension conditioning (Bitterman *et al.*, 1983; Menzel, 1990). All subjects were exposed to a single acquisition trial during which odor was paired with sucrose reinforcement. Two groups were conditioned to a 50:50 mixture of two odorants ($A + X$), and the remaining two were conditioned to a pure odorant ($X$) at the same concentration as when it was presented in the mixture to the former group. (1-Hexanol and geraniol were counterbalanced as $A$ and $X$.) All groups were subsequently tested with a single presentation of the same pure odorant ($X$) that was not reinforced (*i.e.*, an extinction trial was performed). Subjects were scored as having responded to odorant $X$ or not; thus the figure shows the response probabilities in the respective groups. This experiment was performed with a low concentration of sucrose in two groups and a substantially higher concentration in the remaining two groups. The response in both mixture-trained groups ($n = 18$ subjects in both cases) is lower than in the respective pure-odorant-trained groups ($n = 24$). However, the difference is significant only when a lower level of reinforcement is used (LOW: $\chi^2 = 5.58$, $P < 0.05$; HIGH: $\chi^2 = 0.69$, NS).

**Table I**

*Summary of experimental designs used in overshadowing (A) and blocking (B) experiments*

| | Pretraining | Blocking | Test |
|---|---|---|---|
| A. PURE ODORANT: | X → sucrose | —[1] | X |
| OVERSHADOW: | A + X → sucrose | —[1] | X |
| B. BLOCK: | A → sucrose | A + X → sucrose | X |
| NOVEL: | N → sucrose | A + X → sucrose | X |
| OVERSHADOW: | —[1] | A + X → sucrose | X |

[1] For an overshadowing experiment there is no training during the second phase of the experiment. The two OVERSHADOW groups are equivalent even though the phase during which no conditioning takes place is shown to be different between A and B.

conditioned to a mixture of stimuli, which for our purposes would be two odorants ($A + X$). The response to one component (*e.g.*, $X$) is then tested, and one frequently finds that the response is diminished relative to when the mixture is tested. A second group (PURE ODORANT) is conditioned to and subsequently tested under identical conditions with $X$. Overshadowing occurs if the response to $X$ is lower in the group trained to the mixture than in the group trained to the pure odorant. Indeed overshadowing occurs in the honey bee under specific conditions of reinforcement (Fig. 1B).

A recent study of cross-adaptation in the honey bee has demonstrated that the overshadowing data can be accounted for by peripheral sensory interaction (Bhagavan and Smith, in prep.). That is, when the sensory cells are adapted to one odorant, the response to the remaining odorant also shows adaptation. Thus there is significant interaction among odorants as they compete for limiting substrates involved in signaling in the antennal system. Although several mechanisms can account for cross-adaptation, these data provide circumstantial evidence to support the interpretation that overshadowing can also be accounted for by afferent interaction in primary signal transduction processes. This interaction would be capable of giving rise to unique qualities of $A + X$ and would produce overshadowing *via* a process represented in Figure 1A. Note, though, that overshadowing can also be accounted for by other processes; for example, by a decrement in the concentration of odorant that occurs between training of $A + X$ and testing of $X$ (the same decrement does not occur in the PURE ODORANT group; Table 1A). Furthermore, the same attention-based models used to account for blocking (see below) can also account for overshadowing (Rescorla and Holland, 1982). Further experimentation will be required to resolve these interpretations of overshadowing in the olfactory system.

Situations in which subjects have little or no prior ex-

perience with stimuli used for conditioning to mixtures (as, for example, in an overshadowing protocol) may provide valuable, albeit conservative, information regarding how the olfactory system is constrained by afferent interaction caused by specific stimulus configurations. The complexity of the peripheral coding system now emerging from molecular studies (Buck and Axel, 1991) would certainly lead us to expect that mixture representations arising from peripheral sensory-level interactions would occur and account for a number of the behavioral effects of mixtures with varying numbers of components (Laska and Hudson, 1993). But do these kinds of studies indicate absolute limits to an animal's ability to discriminate mixture components? The answer to that question is probably "no."

## Blocking as One Solution to the Generalization Problem

Several studies in recent years have shown that prior experience with an odorant can enhance an animal's ability to detect that odorant in a mixture. Experiments involving selective attention in humans have demonstrated that the ability of subjects to perceive a target component can be improved at least in a limited way (Rabin and Cain, 1989; Laing and Glemarec, 1992). In these protocols, human subjects are instructed to attend to one component and then discriminate that odorant from an adulterated version of itself. Under controlled conditions such familiarity can improve the ability of subjects to detect elements of mixtures.

The learning phenomenon called "blocking" is one of several means of studying different kinds of attention in nonhuman animals (Rescorla and Holland, 1982; Rescorla. 1988; Holland and Gallagher, 1995). Blocking occurs when a subject is conditioned to one stimulus ($X$) in the presence of another ($A$) that has been previously paired with the same reinforcer used for subsequent conditioning of the $A + X$ compound. The response to $X$ after such conditioning is typically lower than when the subject receives $A + X$ pairing (*i.e.*, an overshadowing treatment) with no prior conditioning of $A$. This learning paradigm is important because it shows that proper spatial and temporal pairing of $X$ with a reinforcer is not a sufficient condition to increase learning performance to $X$. Furthermore, it allows an animal to generalize from a learned stimulus (*e.g.*, $A$) to a condition in which $A$ occurs embedded in a different blend or background (*i.e.*, $A + X$) that might degrade the animal's ability to recognize the presence of $A$.

In both *Limax* (Sahley *et al.*, 1981) and honey bees (Smith and Cobey, 1994), blocking has been demonstrated among odorants in mixtures. That is, prior learning about one odorant will block learning about a new odorant when the latter is subsequently provided in a bi-

nary mixture with the first. Both studies incorporated several control procedures (Table 1B). In the honey bee, subjects in group BLOCK were pretrained with several conditioning trials during which odorant $A$ was forward-paired with a sucrose $US$. One control group of subjects (NOVEL) received equivalent pretraining to a different, novel odorant in order to equilibrate exposure in this group to odorant and to the $US$. A second control group (OVERSHADOW) received no pretraining. All groups received equivalent training to the $A + X$ mixture in the subsequent blocking phase. Finally, all groups were tested for their responses to odorant $X$.

The results demonstrate that the response to $X$ is significantly lower in group BLOCK than it is in groups NOVEL or OVERSHADOW (Fig. 2). That is, acquisition to odorant $X$ is blocked or at least significantly retarded when it occurs in a context in which the reinforcer is already adequately predicted. Note that groups did not differ in their exposure to odorant $X$; all of them received equivalent exposure to $X$ in a mixture with $A$. Also note that the level of response in the OVERSHADOW group already represents a decrement in responding (see Fig. 1B) and that the blocking protocol *increases* the level of this effect; that is, the response to $X$ is lower in group BLOCK than it is in group OVERSHADOW.

Several control procedures have shown that simple exposure to the $US$ and to odorant $A$ is not sufficient to produce blocking. When $A$ is either backward-paired or explicitly unpaired with the $US$ in the pretraining phase (that is, using pairing conditions that would not be expected to build up excitatory associative strength to A but would equilibrate exposure to it across groups), blocking did not occur (Sahley *et al.*, 1981; Smith and Cobey, 1994). Therefore, blocking results specifically from forward- (associative-) pairing of odorant $A$ with the $US$ and not from a nonspecific process such as cross-adaptation of sensory cells responsive to $X$ by pre-exposure to $A$. Finally, it should be noted that the decrement in concentration that occurs in an overshadowing experiment, and which could potentially account for overshadowing, occurs equally across all groups in a blocking experiment. Therefore, even if that decrement contributes to overshadowing, it cannot account for differential response levels in a blocking experiment.

It is impossible for the generalization decrement model of Hull (1952) to account for the blocking effect in general and particularly for its specificity to the forward-pairing condition (Pearce, 1987). Why should prior forward-pairing *increase* an overshadowing effect that is, according to that model, due to peripheral interactions? Furthermore, sensory adaptation to odorant $A$ during pretraining could affect the subjects' responses in the blocking protocol in different ways depending on the level of interaction in the antennal system. Because such
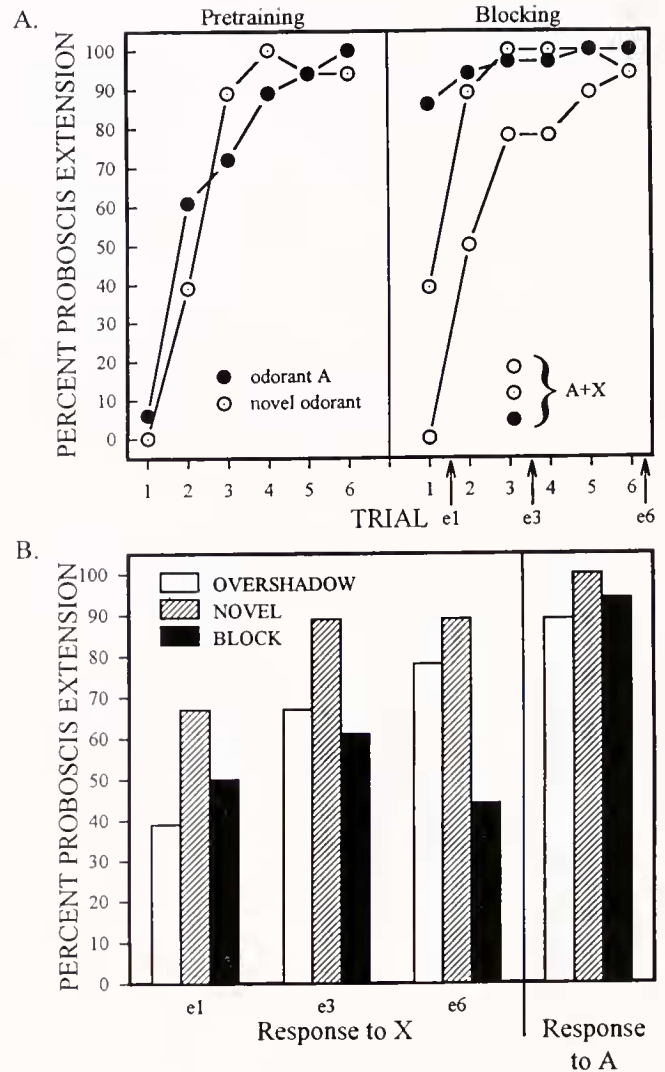


Figure 2.   Summary of acquisition and extinction testing in a blocking experiment. (A) Subjects in groups NOVEL and BLOCK were conditioned to a novel odorant or to odorant $A$, respectively, as in Figure 1B, except six forward-pairing acquisition trials were used in the pretraining phase. All groups received six trials with the $A + X$ mixture in the blocking phase. Geraniol and 1-hexanol were counterbalanced as $A$ and $X$, and 2-octanone was used as the novel pretraining odorant. Eighteen subjects were selected and randomly assigned to each group. In order to assess responses to odorant $X$, all subjects received extinction trials with odorant $X$ after the first, third (e3), and sixth (e6) trials in the blocking phase. In addition, after all extinction testing was complete subjects received a final extinction trial with odorant $A$ to determine whether differences in responding to $X$ might be due to a more general mechanism (*e.g.*, low motivational states) than to blocking. (1.25 $mol \cdot l^{-1}$ sucrose was used for reinforcement throughout the experiment.) (B) The emergence of a blocking effect throughout the course of the blocking phase. Response probabilities to odorant $X$ in groups OVERSHADOW, NOVEL, and BLOCK are shown at e1, e3, and e6. The response probability of group BLOCK is significantly lower that those of groups NOVEL and OVERSHADOW at e6 ($\chi^2 = 2.118$, $P < 0.01$) but not at e1 ($\chi^2 = 2.82$, NS) or at e3 ($\chi^2 = 4.28$, NS). One-trial blocking—that is, a significant difference among groups at e1—occurs under other conditions of reinforcement (Smith, in prep.). Groups do not differ in response probabilities to odorant $A$ ($\chi^2 = 2.12$, NS).

a nonassociative effect could not be detected (Smith and Cobey, 1994), other mechanisms that give rise to blocking should be investigated. Indeed several behavioral models have been invoked to explain the blocking effect: some involve changing levels of attention to the CS or the US, whereas others are based on recall failure (Rescorla and Holland, 1982; Spear et al., 1990). These models still need to be tested in more detailed behavioral analyses, particularly in regard to the emergence of the blocking effect after a single conditioning trial with the mixture (Fig. 2).

Clearly there are several means that animals might employ to extract and thereby detect components of complex olfactory signals. Thus the point made here is not that blocking is the only tactic available for analyzing mixtures. Specific adaptation of sensory receptors for one mixture element can enhance the ability to detect the remaining elements (Cain and Polak, 1992). Laing et al. (1994) have also shown that humans are capable to some extent of distinguishing between fast and slowly processed signal elements. In other words, mixtures can be analyzed perceptually according to the temporal qualities of the components. This latter kind of processing may be particularly useful when the elements of a signal show temporal fluctuations that are uncorrelated to background odors (Hopfield, 1991). The point that must be addressed is how these rules for processing odorant mixtures, particularly the ones that involve attention-like, flexible processing like blocking, are implemented in the CNS.

## Implications for Synaptic Plasticity in the Olfactory Lobes

Although odorant blocking may serve the same function as the pheromone system, the neural mechanisms underlying the two systems must be very different. The blocking system would have to involve a greater degree of, or at least different kinds of, synaptic plasticity, which might be expected even in the more peripheral levels of olfactory processing (e.g., the olfactory/antennal lobes). Thus a comparison of the pheromone and blocking systems from the behavioral to neural and molecular levels should provide insight into the multiple means through which the nervous system can solve the same problem inherent in finding resources.

Can we speculate as to where this synaptic plasticity might occur such that it gives rise to blocking? As already mentioned, because of its specific, associative nature, blocking seems unlikely to arise via known sensory mechanisms in the antennal system (Smith and Cobey, 1994). For example, if blocking had not been specific to the forward-pairing condition, it could have been explained by cross-adaptation of X sensory cells by pre-exposure to A. But in the absence of that result, why would forward-pairing of A with the US, but not the other means of pairing the same two stimuli, decrement the response of sensory cells activated by odorant X when it is mixed with A in the blocking phase? If cross-adaptation could explain olfactory blocking, why would pretraining with a novel odorant not produce blocking?

Therefore, the next level of sensory processing at which synaptic plasticity might occur and give rise to the associative, forward-pairing effects of blocking would be in the antennal lobe (AL; Flanagan and Mercer, 1989; Linster and Masson, 1996), which is structurally analogous to the olfactory bulb of vertebrates (Shepherd, 1991). As sensory axons enter the AL, they project to glomeruli, within which all known synaptic interactions with interneurons in the brain take place (Homberg et al., 1989). It is here that projection neurons, the anatomical invertebrate equivalent of mitral cells, receive input from sensory neurons, although the exact mechanism of this input is still unknown in invertebrates. In addition to these two types of cells, local interneurons are also involved in input/output relationships within glomeruli. One such class of local interneurons, which has arborizations limited to the AL, is GABAergic and presumably capable of spreading inhibition either globally within the AL or throughout a limited subregion (Flanagan and Mercer, 1989; Homberg et al., 1989). Such inhibition is crucial for the ability of projection neurons to track, for example, temporal patterns in pheromone stimuli (Christensen and Hildebrand, 1988).

One other type of interneuron, which has recently been physiologically and immunocytochemically characterized, plays a modulatory role in several brain neuropils (Hammer, 1993). In recordings made from arborizations of this neuron in the mushroom bodies, which are downstream from the ALs, Hammer (1993) has shown that this neuron responds very little to odorant stimulation prior to association of odorant with a US, but that the odorant response increases after forward-pairing. These data indicate that this neuron, named VUMmx1, is capable of representing the US in neural models of associative conditioning, and thus it is an essential element in an associative network in the brain.

The VUM neuron also arborizes extensively within most if not all of the glomeruli within the AL (Hammer, 1993). If this neuron is capable of providing a neural representation of the US and thus mediating synaptic plasticity within the mushroom bodies, then it might be involved in similar associative modification within the AL. Although the argument presented here is only circumstantial, precedents from studies of vertebrates indicate that synaptic plasticity can alter the neural representation of an odorant in the accessory olfactory bulb (Brennan et al., 1990) and in the olfactory bulb of rats (Leon,

1992; Sullivan and Wilson, 1991; Wilson and Sullivan, 1991) and sheep (Kendrick, 1995).

How might this synaptic plasticity alter the neural representation of odorant $A$ during the pretraining phase? Voltage-sensitive-dye recordings from the salamander olfactory bulb show specific spatial and temporal patterns of glomeruli activation when an odorant is presented (Cinelli *et al.*, 1995). It could be that these patterns change as a result of association of the odorant with reinforcement. The activation of glomeruli specific to an odorant at a given concentration could be enhanced; new glomeruli could be recruited; or some aspect of the temporal pattern such as speed or oscillation (see Laurent, 1996; Laurent and Davidowitz, 1994) could be changed. Even if the pattern of excitation did not change, the pattern of local inhibitory transmission might be altered as a result of changes in synaptic drive to inhibitory interneurons.

This is only a partial list of what might be affected by associative conditioning, but it indicates some changes we might search for to test the hypothesis proposed here. The result of any such change could be that patterns of lateral inhibitory transmission would be substantially altered as a result of conditioning. If this inhibition is strengthened, then it might be capable of suppressing a representation evoked for odorant $X$ when it is subsequently added to pretrained odorant $A$. This kind of mechanism would give rise to a blocking effect because, if activation of elements corresponding to odorant $X$ is prevented by the activation of those corresponding to $A$, then $X$ might not be as capable of entering into an association with the reinforcer.

In summary, the mechanisms underlying olfactory blocking may be a means through which the peripheral olfactory system, which includes the AL, deals with the high dimensionality of the input signal from the peripheral sensory system. By acting like a filter of sorts, blocking could cause the representation of a mixture to be biased, or *conditioned*, to be much more like that of a few elements that are, for one reason or another, the most important elements of the signal. A mixture of $A + X$ might be perceived to be much more $A$-like after pretraining with the latter element. This reduction in dimensionality of the input might ease the processing load placed on neuropils, such as the mushroom bodies, that are downstream from the AL and must also integrate information from other sensory modalities into the olfactory information coming from the AL. The end result would be stronger generalization from a conditioned odorant to a mixture that contains that odorant.

## Conclusions

The type of attention system that gives rise to blocking is bound to be different from more cognitive models of attention studied in selective-attention protocols. Nevertheless, this blocking protocol provides access to studies of flexible processing of stimulus mixtures in all animals. In the end we should not be surprised if blocking cannot always recover information about an odor as it is embedded in different backgrounds. But the effect may simply bias the mixture representation to make whatever task is at hand (*e.g.*, stimulus generalization) easier for a later stage of processing. And the results can, as I have attempted to show, provide testable hypotheses about how blocking can be implemented in the CNS. At this point the model proposed above needs to be more thoroughly vetted mathematically and experimentally. But modification in the AL must also be investigated as explanations of the blocking effect are sought in other brain regions downstream from the AL. This model I have proposed may seem to some like too much speculation about behavioral data. But, as Dethier wrote, the study of behavior is, after all, an *exciting game of wits!*

## Acknowledgments

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